

**CHLORACANTHA, A NEW GENUS OF NORTH AMERICAN ASTEREA
(ASTERACEAE)**

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ABSTRACT

Aster spinosus Benth (= *Erigeron ortegae* S.F. Blake), a species widely distributed from Central America into the southwestern United States, is treated as a new genus, **Chloracantha**, with a single species, **C. spinosa** (Benth.) Nesom, *comb. nov.* Although *C. spinosa* produces no terminal resting buds and displays a herbaceous aspect in its permanently green stems without periderm, it behaves more like a shrub in its perennial stems (alive for up to about four growing seasons) with a quickly developed vascular cambium and its production of axillary buds with bud scales. Such a distinctive growth form is not known in any of the more than 500 species of *Aster* or *Erigeron*, the two genera with which the species has been allied, or in any other potentially closely related taxa. Studies of restriction site variation in chloroplast DNA suggest that the closest relative of *C. spinosa* is the genus *Boltonia* and that these two taxa apparently are more closely related to the lineage that includes *Heterotheca* than that of *Aster*; *Erigeron* is yet more distantly related.

KEY WORDS: *Chloracantha*, *Erigeron*, *Aster*, *Heterotheca*, *Boltonia*, Astereae, Asteraceae

Benth (1839) described a distinctive plant from México as *Aster spinosus* Benth., now known to represent a species widely distributed from Central

America through México and into the southwestern United States. Its taxonomic residence until the present has primarily been the genus *Aster* L. The first reservation regarding its placement was registered by Greene (1897), who placed it in *Leucosyris* E. Greene, enlarging that genus from monotypic to ditypic. His rather forced view of the similarity between *A. spinosus* and the type species of *Leucosyris* (*Leucosyris carnosa* [A. Gray] E. Greene = *Linosyris carnosa* A. Gray = *Aster carnosus* [A. Gray] A. Gray ex Hemsl. = *Aster intricatus* [A. Gray] S.F. Blake = *Machaeranthera carnosa* [A. Gray] Nesom) was noted only in the description of "pale green reedy almost leafless stems and permanently white corollas, the rays either very short or wanting" (p. 244). Jones (1980) placed the same two species in sect. *Spinosi* (Alexander) A.G. Jones of *Aster* subg. *Oxytripolium* (DC.) Torr. & Gray, but Jones & Young (1983) soon questioned the close relationship between them. *Linosyris carnosa* was removed from *Aster* and replaced into the monotypic *Leucosyris* by Sundberg (1986); alternatively, Nesom (1990) transferred the species to the genus *Machaeranthera* Nees, but in any case, it clearly is not closely related to *A. spinosus* (see additional comments below). *Aster spinosus* was maintained in *Aster* in a cladistic analysis of the genus (Jones & Young 1983), where *A. spinosus* was positioned as a member of the *Tripolium* group (including the *Oxytripolium* group).

The taxonomic overview of *Aster* provided by Semple & Brouillet (1980) placed *A. spinosus* with *A. pauciflorus* Nutt. in an informal group of two species they referred to as "subg. *Leucosyris*." On the basis of morphology, hybridization experiments, and chromosome number of $n = 9$, Sundberg (1986) concluded that *A. pauciflorus* was an isolated element within *Aster*, perhaps with a portion of its phylogenetic roots near *Machaeranthera* sect. *Psilactis* (A. Gray) Turner & Horne (= *Psilactis* A. Gray). The recent molecular studies by Morgan (1990) have indicated that *A. pauciflorus* is indeed closely related to both the *Oxytripolium* group of *Aster* and *Psilactis*, which also has proved to be closely related to *Aster*. *Aster spinosus* is not part of the phylad that includes *Aster* and *Psilactis*, according to the molecular data.

A morphological similarity between *Aster spinosus* and the genus *Erigeron* was early recognized by Blake (1924), who described one of the geographical variants of the species as *E. ortegae* S.F. Blake, not realizing that it was conspecific with a previously described and well known species. In a study of *Aster* subg. *Oxytripolium* and taxa historically included with it, Sundberg (1986) also perceived a more comfortable fit for *A. spinosus* within *Erigeron* and placed it there, using Blake's epithet ("ortegae") and an accompanying set of varietal nomenclature. He annotated specimens with these names, but his proposed taxonomic changes and new varietal taxa have not been formalized.

Nesom (1989a) hypothesized that the closest relative of *Aster spinosus* was the North American *Erigeron oxyphyllus* E. Greene, and in collaboration with S. Sundberg, created a new section for the two as *Erigeron* sect. *Spinosi*

(Alexander) Nesom & Sundberg. *Erigeron byei* Sundberg & Nesom, a species recently described from northwestern México, was tentatively added as a third species to this group. *Erigeron oxyphyllus*, however, has proved to be a true *Erigeron*, one of the thirteen species of *E. sect. Pycnophyllum* Cronq., closely centered around *E. fohosus* Nutt. (Nesom 1991b). The position of *E. byei* remains equivocal (see comments below).

Most recently, on the basis of restriction site analysis of chloroplast DNA among a wide selection of genera of North American Astereae, Morgan (1990) discovered that *Aster spinosus* is phyletically removed from true *Aster* and even further distant from *Erigeron*; instead, it appears to be a weakly related, basal member of the much more strongly defined phylad that includes *Heterotheca* Cass., *Pityopsis* Nutt., *Chrysopsis* (Nutt.) Ell., *Bradburia* Torr. & Gray, *Osbertia* E. Greene, and *Croptilon* Rafin. Morgan's data included *Aster spinosus* and *Croptilon*; Suh's analysis (1989), which included all of the genera above except *Osbertia* and *Aster spinosus*, was of primary significance in defining the *Heterotheca* phylad. He found that the genus *Boltonia* L'Herit., like *A. spinosus*, is best placed as a weakly associated basal member of this same lineage. A morphologically based hypothesis of the phylogeny of this group will be presented by Nesom (1991a), and a summary of this and the other broad phyletic lines that exist within North American Astereae, based on cpDNA restriction site data and emphasizing primary groupings of genera rather than the more tenuously defined phylogenetic connections between these groups, is presented in Nesom, et al. (1990).

Although the molecular data provide evidence that the phylogenetic origin of *Aster spinosus* is independent of *Aster* and *Erigeron*, the relatively generalized features of capitular, floral, and fruit morphology of this species have not provided an unequivocal basis for an alternative placement or even its rejection from either genus. In the present paper, we add critical observations regarding the morphological differences between *A. spinosus* and *Machaeranthera carnosa* as well as all species of both *Aster* and *Erigeron*. A technical description of the species follows its formal nomenclatural treatment at the end of the paper; a more detailed narrative of the distinctive vegetative features of *A. spinosus* is presented here in order that it can be contrasted with its putative relatives.

Vegetative morphology of Aster spinosus

The following observations were made by the first author from a vigorous colony of plants cultivated for five years in the back yard of his residence in Austin, augmented by study of natural populations in Travis Co., Texas, which proved to be essentially identical in growth pattern to the cultivated plants. The latter were begun from rhizomes transplanted from Hays Co., Texas, on the floodplain of the Pedernales River, ca. 1 mile northwest of the Travis Co.

line; a voucher specimen (*Nesom s.n.*) of these plants, showing different stages of growth, is deposited at LL,TEX. Anatomical observations have been made from hand sections of fresh stems.

The first year stems (here referred to as "ramets") arise from stout rhizomes and grow quickly to produce a strictly erect, central axis with numerous, narrowly oblanceolate leaves. On the upper 70-80% of the main stem, each of the axillary buds develops without dormancy directly into a sharply ascending branch, all of which produce a full complement of leaves but no lateral branches. The stems are determinate, and maximum vertical growth appears to be attained first year. Single capitula are produced at many of the stem apices, and, lacking terminal buds, the terminal portions of all stems die at the season's end, leaving long (1-3 dm), thin, dead but persistent branch tips. The lower portions of many of the lateral branches remain alive over the winter, but other of the lower branches die back to near their point of origin at the main stem.

All portions of the stems are distinctively green and glaucous, and these plants have been regarded as "herbaceous," either directly or by implication from the generic description, in almost all published treatments, although they have often been noted to be basally woody. In contrast, Wiggins (1980) and McVaugh (1984) have clearly distinguished it as shrubby or suffrutescent. The first year stems remain flexuous but a vascular cambium is produced very early, and by about 4 weeks the cambium is completely cylindrical. Growth rings are weakly if at all developed, but the stem diameter expands significantly to a maximum of about 9 mm, and the base of the stem becomes particularly woody. A cork cambium apparently never forms, and all stems, including the main axis of each ramet, remain green with a smooth, waxy epidermal surface for their whole life, the cortex and epidermis keeping pace in expansion with that of the secondary xylem. Except for this, the secondary growth is otherwise mostly similar to that of typical woody stems.

On the lower part of the stem, where lateral branches are not produced immediately with the leaves, a small axillary bud (primary bud) is evident at each node. In each of the upper nodes with lateral branches, a second axillary bud (serial bud) is produced. All axillary buds first appear simply as leaf primordia, but by late in the growing season, undeveloped buds (both primary and serial) become enclosed by ca. 8-12, brown sclerified scales 0.5-1.0 mm long with rounded, minutely fimbriate-ciliate margins. Early in the growing season of the second year, most of the (serial) buds on the upper half of the main stem produce fascicles of leaves, these apparently on short shoots, a few of which may elongate into relatively short stems. Both the first set of leaves and the later-produced fascicles are quickly deciduous and most if not all have been shed by the time of flowering. A few of the lower (primary) buds usually open in subsequent years, and the main growth of individual ramets past the second year is mostly limited to short branches produced by these

buds and (primary) buds on the original set of lateral branches. Most ramets do not live past 3 or 4 years; they die and are replaced by new ones from the rhizomes in various parts of the clones.

In some of the geographic races of *Aster spinosus*, the primary lateral branches are characteristically modified into short, stout thorns (the epithet "spinosus" is technically a misnomer). The plants from Texas as well as the rest of the southwestern United States belong to the typical race (Sundberg 1991), where thorns are weaker and less commonly produced.

Flowering occurs in the late summer and fall. The capitula are produced at the stem apices as well as very short (3-15 mm long), bracteate stems that arise from the uppermost buds.

Aster spinosus distinguished from *Machaeranthera carnos*a, *Aster*, and *Erigeron*

The chromosome number of *Aster spinosus* ($n = 9$) separates it from *Machaeranthera carnos*a ($n = 5$, see Nesom 1990b), and despite Greene's hypothesis of close relationship between these two species, they are similar in little else than their shrubby, rhizomatous habit, and even then, the latter produces neither thorns nor axillary buds with bud scales. The subulate leaves of *M. carnos*a, its corollas and phyllaries without orange resinous veins, lance-attenuate style tips, sericeous achenes, basally flattened pappus bristles, and chromosome number are features in common with *Machaeranthera*.

All species of *Erigeron* as well as a large segment of *Aster* have a chromosome number of $n = 9$, but no species of *Aster* or *Erigeron* produces thorns or bud scales. *Aster spinosus* has been placed with the *Oxytripolium* group primarily on the basis of its glabrous stems and leaves, and slender, strictly erect stems, although these species of *Aster* have $n = 5$. Except for the peculiar growth habit, the morphological characters that distinguish it from *Aster* are mostly those that are more similar to *Erigeron*: the lack of green herbaceous apical regions of the phyllaries, the presence of prominent, orange resinous veins in the disc corollas, and deltate collecting appendages of the style branches. The latter feature was the only one specifically mentioned by Blake (1921) in his decision to place *E. ortegae* in *Erigeron* rather than *Aster*.

The genus *Erigeron* has seemed variable enough to accommodate even a species as peculiar as *Aster spinosus*, but continuing study of interspecific relationships within the genus has shown that *E. oxyphyllus*, with which it was associated (Nesom 1989a), is a species closely related to *E. foliosus* (Nesom 1991b). Although it is largely lacking in vestiture, the leaves of *E. oxyphyllus* are basally ciliate, the phyllaries are minutely glandular, and sparsely strigose, the achenes are strigose and 2-4 nerved, and it does not produce a system of spreading, underground rhizomes like that of *A. spinosus*.

Besides its growth habit, the phyllary morphology of *Aster spinosus* is the only feature that is not matched by any species of *Erigeron* or close relatives.

The nearly oblong phyllaries produce hyaline margins that extend about the rounded apex, and the dense concentration of stomates give the lateral surfaces a punctate appearance. The nervation of three parallel veins that has been noted as distinctive cannot be emphasized as an indicator of close relationship, because similar nervation occurs in almost all species of *Trimorpha* Cass. (Nesom 1989b) and *Conyza* L. (Nesom 1990a), both genera apparently closely related to *Erigeron*, as well as a number of species of *Erigeron* in different sections (Nesom 1989a). Three nerved phyllaries are almost certainly primitive among these taxa.

The hypothesis that *Erigeron byei* is closely related to *Aster spinosus* (Nesom 1989a; Sundberg & Nesom 1990) was based heavily on their nearly identical phyllaries, rhizomatous habit, and persistently green glabrate stems and leaves. Plants of *E. byei*, however, are diminutive relative to *A. spinosus* and they produce persistent basal leaves and annual stems without axillary resting buds. Further, their achenes are more characteristic of *Erigeron* in the strigose vestiture and (2-3-)4(-5) nerves. The chromosome number of $n = 9$ is of equivocal significance. While we believe that the evolutionary affinities of *E. byei* may yet prove to lie with *A. spinosus*, outside of *Erigeron*, there is insufficient evidence at present to make the nomenclatural transfer formal.

Aster spinosus distinguished from taxa of the *Heterotheca* lineage

The molecular data of Morgan and Suh, as noted above, indicate that *Aster spinosus* and *Boltonia* are apparently more closely related to the *Heterotheca* lineage than any other, although they are associated with it as basal members. Except for these two taxa, however, the other genera closely related to *Heterotheca* produce prominently pubescent vegetative organs, yellow ray flowers, disc style branches with linear-lanceolate appendages, and densely strigose-sericeous achenes. *Boltonia* and *A. spinosus* are strikingly similar between themselves in their glabrate stems and leaves, quickly deciduous leaves, white ray flowers, disc style branches with deltate appendages, and their glabrous or minutely pubescent achenes. Both have a chromosome number of $n = 9$; this number is also hypothesized to be primitive within the *Heterotheca* lineage (Nesom 1991a). *Boltonia* differs from *A. spinosus* in its flattened, weakly to strongly winged achenes with a pappus of two thick awns and series of much shorter, thinner bristles, and while the plants are also rhizomatous and perennial, they produce shorter rhizomes and do not form large colonies like *A. spinosus*. The strictly annual stems of *Boltonia* do not produce axillary buds or thorns. *Boltonia* includes five species, all restricted to the eastern United States (see Anderson 1987 for a review of the genus), where they are mostly allopatric with *A. spinosus*.

Perenniality in *Aster*, *Erigeron*, and other American Astereae

All species of *Aster* (excluding subg. *Conyzopsis* [Torr. & Gray] A. Gray = *Brachyactis* Ledeb.) are perennial except several of sect. *Oxytripolium* and *Psilactis* (= *Machaeranthera* sect. *Psilactis*, see previous comments). The above ground parts are primarily herbaceous, but some species produce stems that are woody at least at the base (e.g., *A. novae-angliae* L.). No resting buds with bud scales are produced, however, and in all taxa the vegetative parts die back to ground level at the end of each season. The perennating meristems are restricted to the shoot apex.

The situation is similar in *Erigeron*, where most species also are perennial, but it is a larger genus including a greater number of species that produce woody stems. Species with woody bases are found in a number of different sections, and even in sect. *Olygotrichium* Nutt., where the species are characteristically annual (Nesom 1989a), *E. modestus* A. Gray and *E. bigelovii* A. Gray are clearly perennial and produce woody stem bases. The species of sect. *Polyactis* (Less.) Nesom are primarily perennial with woody rhizomes and lower stems; in *E. polycephalus* (Larsen) Nesom of that section, the woodiness extends further up the stems so that the plants may be referred to as "subshrubs." Some insular species of *Erigeron* of disparate phylogenetic origin within the genus have developed a subshrubby, "rosette" habit. These plants have long, mostly unbranched stems with leaves clustered near the stem tips (see Nesom 1989a, following "*Darwiniothamnus* Harling," for further comments and examples). In all of these species, however, the perennating buds are restricted to the shoot apices, there are no axillary resting buds, and there are no buds at all enclosed by bud scales.

The perennial species of the *Heterotheca* lineage are similar in growth habit to those in *Aster* and *Erigeron*. Even among other genera of other American Astereae that produce true shrubs, such as *Acamptopappus* A. Gray, *Baccharis* L., *Chrysothamnus* Nutt., *Hazardia* E. Greene, *Isocoma* Nutt., *Machaeranthera* (e.g., *M. restiformis* B. Turner and *M. carnosa*), and *Xylorhiza* Nutt., as well as many others, new growth is mostly or completely initiated from the meristems of the shoot apices. Lateral buds are difficult to discern and bud scales even more so, perhaps partially because most specimens are collected during periods of growth soon after the breaking and expansion of meristems. In any case, we have not seen what could be unequivocally interpreted as bud scales among any of these. Of the American genera with a shrubby habit, some species of *Baccharis* produce determinate stems and are similar in general aspect to *Aster spinosus*, but in all species of the former examined, including a number from both North and South America, we have seen only unprotected primordia in the leaf axils.

A new genus for *Aster spinosus*

We conclude that *Aster spinosus* is morphologically anomalous within the boundaries of both *Aster* and *Erigeron*, and there is no evidence for its putatively close relationship with *Machaeranthera* (*Leucosyris*) *carnosa*. It is not impossible that the distinctive features of *A. spinosus* might have arisen from ancestors in one or the other of these genera, but the studies of cpDNA restriction site variation do not support this hypothesis. Although these are the only genera with which it has been formally associated, molecular evidence indicates that it is probably more closely related to the genus *Boltonia* and then to the lineage that includes *Heterotheca* and its relatives. We acknowledge the phyletic isolation of *A. spinosus* and propose to accommodate it within the tribe Astereae by erecting a new genus, the name chosen in reference its evergreen, thorny ("spiny") stems.

Chloracantha Nesom, Suh, Morgan, Sundberg, & Simpson, *gen. nov.* TYPE: *Chloracantha* (*Aster*) *spinosus* (Benth.) Nesom.

Aster sp.-group *Spinosi* Alexander in Small, *Man. Southeastern Fl.* 1365. 1933, in clave. TYPE: *Aster spinosus* Benth. *Aster* sect. *Spinosi* (Alexander) A.G. Jones, *Brittonia* 32:233. 1980. *Erigeron* sect. *Spinosi* (Alexander) Nesom & Sundberg, *Phytologia* 67:85. 1989.

Aster ac Erigeronti similis sed caulibus spinosis perennibus semipervirentibus viventibus per annos 2-4 et gemmis axillaribus ad maturitatem squamis obtectis differt.

Chloracantha spinosa (Benth.) Nesom, *comb. nov.* BASIONYM: *Aster spinosus* Benth., *Pl. Hartweg.* 20. 1839. TYPE: MÉXICO. Aguascalientes (according to McVaugh 1984): [ca. 1836], *K.T. Hartweg 148* (HOLOTYPE: K, MICH-photo!, TEX-photo!; Isotypes: BM, CGE, GH!). *Leucosyris spinosa* (Benth.) E. Greene, *Pittonia* 3:244. 1897.

Erigeron ortegae S.F. Blake, *Proc. Biol. Soc. Washington* 37:55. 1924. TYPE: MEXICO. Sinaloa: Balboa, Jan 1923, *J.G. Ortega 4974* (HOLOTYPE: US!).

Glabrous or glabrate, glaucous, perennial subshrubs forming large clones, spreading by stout rhizomes that eventually becoming densely woody and irregularly thickened, the main stems strictly erect, 0.5-1.5(-2.5) m tall, with lateral branches sharply ascending, the latter sometimes modified as thorns. Leaves all cauline, alternate, uninerved, 1-5 dm long, oblanceolate, entire or very rarely with 1-2 pairs of small teeth, early deciduous, glabrous except the

margins sometimes sparsely ciliate and the upper surface sometimes with scattered minute hairs. Heads broadly turbinate to hemispheric, produced singly in loose, corymboid panicles; buds erect; receptacles shallowly convex, smooth to shallow foveolate, epalcate; phyllaries strongly graduated in (3-)4-5 series, the inner 4.5-7.5 mm long, each with (1-)3(-5), parallel, orange resinous veins, oblong elliptic to lanceolate, apices usually rounded but sometimes lanceolate, the margins (including the apex) hyaline. Ray flowers 10-33 in a single series, pistillate, fertile, the corollas 4-8(-11) mm long, the ligules (0.5-)1-2 mm wide, white, sometimes bluish tinged, coiling at maturity. Disc flowers numerous, hermaphroditic, fertile, the corollas yellow with orange resinous veins, narrowly funnelform, (3.2-)3.5-6.0 mm long, the lobes deltate; style with a bulbous base, the branches with deltate to triangular collecting appendages 0.1-0.2 mm long. Achenes glabrous, slightly compressed, 1.5-3.5 mm long, with 5(-6), whitish to golden brown nerves; carpopodium 4-8 cells high; pappus of 30-60 whitish, slender, terete, barbellate bristles in ca. 2 series, about as long as the disc corollas, usually with a few with much shorter outer setae. Chromosome number, $n = 9$ pairs (summary of original and previously published counts in Sundberg 1986).

Panamá to Guatemala, widespread in México, southwestern United States from southern California as far north as southern Utah and east to Oklahoma, Texas, and Louisiana; in a variety of habitats, though most commonly near water, mostly at low elevations but at some sites up to nearly 2000 m; flowering Jun-Oct in the northern part of its range, nearly all year in the south.

Geographic variation within *Chloracantha spinosa* has been studied by Sundberg (1986), who presents its infraspecific taxonomy in this volume (Sundberg 1991).

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ERRATUM-*ISOCOMA PLURIFLORA* (TORR. & A. GRAY) E. GREENE

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In a recent paper (Taxonomy of *Isocoma* (Compositae: Astereae), *Phytologia* 70:69-114. 1991.), I consistently treated the name of a common species from the south central United States and México as *Isocoma plurifolia*. I am grateful to Dr. A. Cronquist, however, for pointing out that the correct epithet is "*pluriflora*" rather than "*plurifolia*," based on *Linosyris pluriflora* Torr. & A. Gray, and the correct name in *Isocoma* is *I. pluriflora* (Torr. & A. Gray) E. Greene.